Mathematical Biology

Olaf Dreyer · Raymond Puzio

Allometric scaling in animals and plants

Abstract. In this paper we give a derivation for the allometric scaling relation between the metabolic rate and the mass of animals and plants. We show that the characteristic scaling exponent of 3/4 occurring in this relation is a result of the distribution of sources and sinks within the living organism. We further introduce a principle of least mass and discuss the kind of flows that arise from it.

1. Introduction

In 1947 M. Kleiber [5](see also [8]) found a remarkable relationship between the metabolic rate B and the mass M of animals or plants. The data showed that these two quantities are related by an allometric scaling law of the form

$$B = B_0 M^\gamma, \tag{1}$$

where the scaling exponent γ is to a very good approximation given by 3/4 and B_0 is some constant (see figure 1). We will refer to it as Kleiber's law.

Since this law has been found it has been a challenge to explain the scaling exponent 3/4 which is of the curious form $D/(D + 1)$, where D is the dimension of space. The first successful attempt was made by T. A. McMahon [7] who derived the law from his principle of elastic similarity. The following attempts concentrated on special properties of the transportation networks inside animals or plants that are responsible for distributing blood or sap respectively to the cells of the organism [12][1]. We will show that less detailed assumptions about the system have to be made in order to arrive at the scaling law.

In [3] it has been shown that the properties of the transportation network are not decisive for the characteristic exponent of $D/(D+1)$. It is rather the distribution of sinks and sources in a living animal or plant that is responsible for the occurrence of this particular scaling exponent. The fact that animals and plants are what we call constant source systems is what gives the characteristic scaling exponent. We

O. Dreyer: Center for Gravitational Physics and Geometry, The Pennsylvania State University, 104 Davey Laboratory, University Park, PA 16802–6300, USA. e-mail: dreyer@phys.psu.edu

R. Puzio: Department of Physics and Astronomy, University of Mississippi, 108 Lewis Hall, University, MS 38677, USA. e-mail: puzio@phy.olemiss.edu
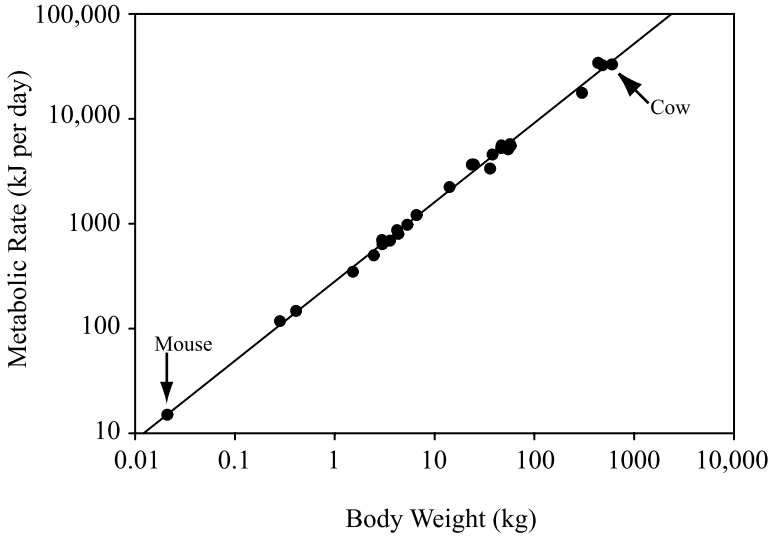
Fig. 1. A double logarithmic plot of the metabolic rate vs. the mass for an assortment of animals. The straight line shows a scaling exponent of 3/4. The data for the plot is taken from [5].

will give a precise definition of a constant source system and will show that the scaling law follows.

After Kleiber's discovery allometric scaling laws were found in other systems as well. One example is the drainage basin of a river. In [1] it is shown that the mass of the river and the area of the drainage basin follow a scaling law with an exponent of 2/3. An example of a one-dimensional system that exhibits scaling is given in [3] where the flow through a tube is investigated. It is found that the amount of water in the tube and its length are related by a scaling law with exponent 1/2. Our derivation of the scaling law applies to all these systems.

The distribution of sinks and sources in an organism does not in general fix the flow of blood or sap uniquely. One may thus ask for the conditions that uniquely determine the flow. It seems reasonable to require here that the mass of the transportation network is as low as it can be while still providing the organism with the required nutrients. We will discuss the kind of flow that follows from this requirement.

The paper is thus organized as follows. In the first section we introduce constant source systems and give a mathematically precise definition of them. In the second section we derive the scaling exponent from general properties of constant source systems. We then introduce a variational principal that corresponds to asking that the mass of the organism be the minimal mass possible and derive the flow that results from this principle. We further give a few examples. We close with some general remarks.

2. Constant source systems

In both animals and plants nutrients have to be supplied to the whole organism from a central source. In the case of animals this source is the heart; for plants it is the stem that connects the plant to its roots. It is also true that the amount of nutrients that are required per volume is roughly constant throughout the organism. As in [3] we conceptualize these two properties, the central source and the constant distribution of sinks, in the following definition:

Definition 1. *A **constant source system** is a triple $(V, \vec{j}, c)$, where V is a regular domain[1] in R^D which contains the origin, $\vec{j}$ is a vector field defined in a neighborhood of V with the possible exception of the origin, and $c \in R$ is a constant such that*

$$\nabla \cdot \vec{j} = A_c \delta_0 + c \tag{2}$$
$$\vec{j}_\perp|_{\partial V} = 0, \tag{3}$$

where $A_c \in R$ is a constant, δ_0 is the Dirac delta distribution[2] at the origin, and $\vec{j}_\perp$ is the component of $\vec{j}$ that is perpendicular to the tangent space of ∂V.

The reason why we index the constant A_c with c is that it is determined by c, as the following lemma shows:

Lemma 1. *Let $(V, \vec{j})$ be a constant source system. Then*

$$A_c = -c \operatorname{Vol}(V). \tag{4}$$

Proof. From Gauss's theorem we infer

$$\int_V \nabla \cdot \vec{j} \, dv = \int_{\partial V} \vec{j} \, d\sigma = 0, \tag{5}$$

since $\vec{j}$ is perpendicular to the normal of the boundary ∂V. On the other hand it follows from equation (2) that this integral equals $A_c + c \operatorname{Vol}(V)$. Our result thus follows.   □

The definition deserves some discussion. Equation (2) describes the sources of the flow $\vec{j}$. As we have discussed above it consists of two terms; the central source represented by the delta distribution and a constant distribution of sinks represented by the constant c. Equation (3) expresses the fact that no blood or sap leaves the organism. The flow $\vec{j}$ is thus required to be parallel to the boundary ∂V of V.

Before turning to the allometric scaling law we give a simple example of a central source system.

---

[1] V is thus a manifold with boundary contained in R^D. For more details see [11, p. 145]
[2] For more information about distributions see [10].

Example 1. Let V be the ball B_R of radius R around the origin in R^D. If we restrict ourselves to spherically symmetrical solutions we can easily find the flow $\vec{j}$. It follows from spherical symmetry that the flow $\vec{j}$ has to be radial. Using Gauss's theorem as in the previous lemma we can calculate the magnitude $j(r)$ of the flow $\vec{j}(\vec{r})$ for $r < R$.

We get

$$\sigma_D \, r^{D-1} \, j(r) = c \, \omega_D \, (R^D - r^D), \tag{6}$$

where σ_D and ω_D are the surface area and volume of the D - dimensional unit ball respectively. The flow is then

$$\vec{j}(\vec{r}) = \frac{c}{D} \left(1 - \frac{R^D}{r^D} \right) \vec{r}. \tag{7}$$

Here we have used the fact that the quotient of ω_D and σ_D is equal to the inverse of D. It is easily checked that $(B_R, \vec{j}, c)$ is a constant source system in R^D.

3. Allometric scaling

In this section we want to derive the allometric scaling law along the lines of [3]. To this end we have to identify the quantities that correspond to the metabolism B and the mass M of the organism in our model.

The metabolism B of the organism is proportional to the amount of nutrients delivered to the system. Since we assume that we have a constant distribution of sinks described by the constant c in equation (2) this amount is proportional to the volume of V. The metabolism is then proportional to

$$\tilde{B} = \text{Vol(V)}. \tag{8}$$

To find the quantity corresponding to the mass of the animal we have to use a relation between the mass of the animal and the mass of the blood or sap contained in the animal. It has been found [9] that these quantities are proportional to each other. It thus suffices to calculate the mass of the blood or sap contained in the organism. Given the flow $\vec{j}$ this can be done using the equation

$$\vec{j} = \rho \, \vec{v}, \tag{9}$$

which relates the flow to the density ρ of the flowing medium and its velocity $\vec{v}$. We now make a simplifying assumption. We assume that the velocity of the flowing medium is roughly constant throughout the organism. This assumption is however not necessary for the derivation of the scaling law. The constant velocity can be thought of as the average velocity of the medium. Under this assumption the mass of the blood or sap is then obtained by integrating the magnitude of $\vec{j}$ over the volume V. The mass of the animal is then proportional to the quantity

$$\tilde{M} = \int_V |\vec{j}| \, dv. \tag{10}$$

Now that we have identified the quantities $\tilde{M}$ and $\tilde{B}$ we want to investigate how they change if we scale the region V by some positive parameter $s > 0$, i.e. replace V by $s \cdot V$. The crucial observation here is made in the following proposition (see figure 2):
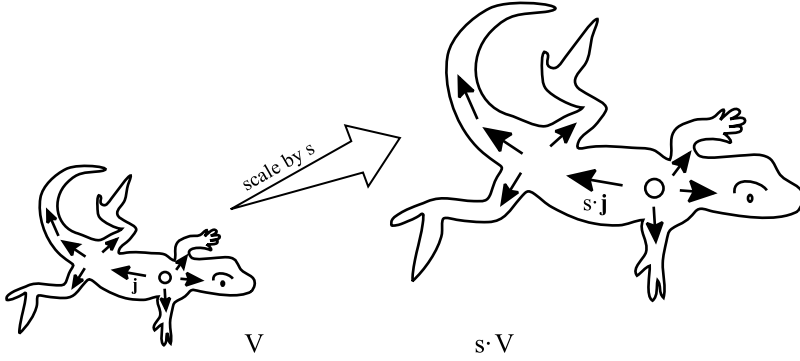
Fig. 2. The arrows in this figure represent the flow of the medium transporting the nutrients inside the lizards. The key observation that leads to the allometric scaling law is that if $\vec{j}(\vec{r})$ is a flow in the unscaled region V then $s\vec{j}(\vec{r}/s)$ is a flow for the scaled region sV. This is represented in the figure by arrows of increased length in the bigger of the two lizards.

Proposition 1. *Let V be a regular domain in R^D. Then $(V, \vec{j}(\vec{r}), c)$ is a constant source system if and only if $(sV, s\vec{j}(\vec{r}/s), c)$ is a constant source system, for all $s > 0$.*

Proof. The gradient of $s\vec{j}(\vec{r}/s)$ is given by

$$\nabla \cdot s\vec{j}(\vec{r}/s) = (\nabla \cdot j)(\vec{r}/s). \tag{11}$$

The scaled flow thus gives rise to a constant source system if and only if the unscaled flow does.   □

This proposition has the allometric scaling law as a corollary:

Corollary 1. *Let $(V, \vec{j}, c)$ be a constant source system. Let $\tilde{M}_1$ and $\tilde{B}_1$ be the quantities introduced in equations (8) and (10) respectively. The corresponding quantities $\tilde{M}_s$ and $\tilde{B}_s$ calculated for the scaled constant source system $(sV, s\vec{j}(\vec{r}/s), c)$ given by proposition 1 then satisfy*

$$\tilde{M}_s = s^{D+1} \tilde{M}_1 \tag{12}$$

$$\tilde{B}_s = s^D \tilde{B}_1 \tag{13}$$

Furthermore $\tilde{M}_s$ and $\tilde{B}_s$ are related through the allometric relation

$$\tilde{B}_s = \tilde{B}_0 \tilde{M}_s^{\frac{D}{D+1}}, \tag{14}$$

for a constant $\tilde{B}_0$ and all $s > 0$.

Proof. Since the volume scales like s^D we immediatly find equation (13). Equation (12) follows from the scaling behaviour of the flow $\vec{j}$ which was derived in proposition 1. A simple transformation of the integration variable gives

$$\tilde{M}_s = \int_{sV} |s\vec{j}(\vec{r}/s)| dv = s^{D+1} \int_V |\vec{j}(\vec{r})| dv = s^{D+1} \tilde{M}_1. \tag{15}$$

Eliminating the scaling parameter s in equations (12) and (13) we find equation (14) where the constant $\tilde{B}_0$ is given by $\tilde{B}_1 / \tilde{M}_1^{D/D+1}$.   □

With our identification of $\tilde{M}$ and $\tilde{B}$ with the mass M and the metabolism B of the organism respectively we recover the allometric scaling relation (1) from equation (14).

A few remarks are in order. To identify our quantity $\tilde{M}$ with the mass M of the organism we had to assume that the velocity of the blood or sap is roughly constant throughout the organism. To develop the allometric scaling law we have to go a little further. We have to assume that the velocity does change much for different species. This assumption has been checked for mammals [4] and is reasonable for plants to assume because the principle behind the transport here is osmosis. The rate of osmosis depends only on the properties of the membrane and the concentration of the solutions and is thus independent of the size and form of the plant. Since Kleiber's law (1) is valid over several orders of magnitude it can not happen that the velocity scales like any appreciable power of the scaling parameter because the speeds involved would become too large.

Another question that we have to address is why nature should choose the scaled flow given in proposition 1 for the scaled region. In the next section we will show that two constant source systems with regions V and sV are both minimal in a sense defined in the next section if and only if they are related in the way described in proposition 1. If nature thus adheres to this optimization principle the scaled flow is chosen and we obtain the allometric scaling behaviour as in equation (1).

4. A variational principle

In this section we investigate the kind of flow that originates from the requirement that the mass of the transportation system is as small as it can be while still providing the organism with nutrients. We formalize this in the following definition.

Definition 2. *Let* $(V, \vec{j}, c)$ *be a constant source system in* R^D. $(V, \vec{j}, c)$ *is called* **minimal** *if and only if there is no other constant source system* (V, j', c) *such that*

$$\int_V |\vec{j}'| \, dv < \int_V |\vec{j}| \, dv. \tag{16}$$

We now want to find the flow $\vec{j}$ of a minimal constant source system. To do this we apply variational methods to the integral occurring in equation (16). Since we are dealing with a constant source system we have to ensure that the flow satisfies $\nabla \cdot \vec{j} = c$ inside of V. This can be achieved by introducing a Lagrange multiplier λ. The variational principle that we get is thus

$$\delta \int_{V - B_0(r)} |\vec{j}| + \lambda (\nabla \cdot \vec{j} - c) \, dv = 0. \tag{17}$$

Because of the singular behaviour of the sources of $\vec{j}$ at the origin we exclude a ball $B_0(r)$ of small but arbitrary radius $r > 0$ around the origin from the region of integration.

The equations arising from this variational principle are given in the next proposition:

Proposition 2. *The Euler – Lagrange equations arising from the variational principle (17) are*

$$\nabla \cdot \vec{j} = c \tag{18}$$

$$\nabla \lambda = \frac{\vec{j}}{|\vec{j}|}. \tag{19}$$

Proof. Carrying out the variation (17) gives

$$\int_{V-B_0(r)} \left(\frac{\vec{j} \cdot \delta\vec{j}}{|\vec{j}|} + \lambda \nabla \cdot \delta\vec{j} + (\nabla \cdot \vec{j} - c)\delta\lambda \right) dv = 0 \tag{20}$$

Since the variation $\delta\lambda$ of λ is arbitrary we immediately find equation (18). Integrating by parts the second term in equation (20) gives the following result for the remaining terms

$$\int_{V-B_0(r)} \left(\frac{\vec{j}}{|\vec{j}|} - \nabla\lambda \right) \cdot \delta\vec{j} \, dv = 0. \tag{21}$$

Because $\delta\vec{j}$ is arbitrary we obtain equation (19).   □

Example 2. The constant source system given in example 1 is minimal. Since the flow is radial it is easy to see that the Langrange multiplier λ in this example is nothing but the radial coordinate r.

In the next section we look for solutions to equations (18) and (19).

Before concluding this section we investigate how minimal constant source systems behave under scaling. As we have alluded to in the last section scaling preserves minimality:

Lemma 2. *Let $(V, \vec{j}(\vec{r}), c)$ be a constant source system. It is minimal if and only if $(sV, s\vec{j}(\vec{r}/s), c)$ is minimal for all $s > 0$.*

Proof. Assume that $(V, \vec{j}, c)$ is a minimal constant source system and assume furthermore that $(s_0 V, s_0\vec{j}(\vec{r}/s_0), c)$ is not minimal for some $s_0 > 0$. Then there exists a flow $\vec{j}'$ such that $(s_0 V, \vec{j}', c)$ is a constant source system and

$$\int_{s_0 V} |\vec{j}'(\vec{r})| \, d\vec{r} < \int_{s_0 V} |s_0\vec{j}(\vec{r}/s_0)| \, d\vec{r}. \tag{22}$$

If we perform a change of variables as in the proof of corollary 1 to proposition 1 we find

$$\int_V |\vec{j}'(s_0\vec{r})/s_0| \, d\vec{r} < \int_V |\vec{j}(\vec{r})| \, d\vec{r}. \tag{23}$$

This is a contradiction to our assumption that $(V, \vec{j}, c)$ is a minimal constant source system. The other implication is proved similarly.   □

5. Minimal flows

In this section we want find constant source systems that satisfy equation (19). Taking the square of equation (19) we find

$$\nabla\lambda \cdot \nabla\lambda = 1. \tag{24}$$

This equation has the form of a Hamilton - Jacobi equation for a particle moving in D dimensions. Such equations can be solved using the method of characteristics.

If λ is a solution to equation (24) the characteristics are a congruence of curves with the property that the tangent vector at any point of one of the curves equals the gradient of λ at that point. If the congruence is given by $\sigma(t;s)$, where the parameter s labels the different curves in the congruence and t is the parameter along the curves, this condition translates to

$$\frac{d}{dt}\sigma(t;s) = \nabla\lambda(\sigma(t;s)), \tag{25}$$

for all s and t.

We now want to find the characteristics in our problem.

Lemma 3. *The characteristics for equation (24) are straight lines.*

Proof. Writing equation (24) in coordinates and differentiating with respect to x_j gives

$$\sum_i \frac{\partial}{\partial x_i}\lambda \frac{\partial}{\partial x_j}\frac{\partial}{\partial x_i}\lambda = 0. \tag{26}$$

The jth-component of the second t-derivative of $\sigma(t;s)$ on the other hand is given by

$$\frac{d^2}{dt^2}\sigma_j(t;s) = \sum_i \frac{\partial}{\partial x_i}\frac{\partial}{\partial x_j}\lambda(\sigma(t;s))\frac{d}{dt}\sigma_i(t;s) \tag{27}$$

$$= \sum_i \frac{\partial}{\partial x_i}\frac{\partial}{\partial x_j}\lambda(\sigma(t;s))\frac{\partial}{\partial x_i}\lambda(\sigma(t;s)), \tag{28}$$

where we have used equation (25) twice. Comparing equations (27) and (26) gives

$$\frac{d^2}{dt^2}\sigma(t;s) = 0, \tag{29}$$

from which we infer that the characteristics are straight lines.   □

Example 3. In example 1 the characteristics are of the form $t\vec{\hat{r}}$, where $\vec{\hat{r}}$ is a unit vector in R^D.

We now want to show that this example reflects the general situation. As in the case of the ball the characteristics are lines. For a certain class of regions they are even radial as in the case of the ball. To show this we introduce some technical notations.

Let $p \in V$ a point such that $\vec{j}(p) \neq 0$. Let λ_0 be the value of the function λ at p. Then there exists a neighborhood U of $0 \in R^{D-1}$ and a diffeomorphism f which maps U into V such that

$$\lambda(f(x)) = \lambda_0, \tag{30}$$

for all $x \in U$. The diffeomorphism f gives thus coordinates on the surface defined by $\lambda(q) = \lambda_0$. Since $\vec{j}(p) \neq 0$ we can assume that $\vec{j}$ does not vanish for all $p \in U'$.

Using the diffeomorphism f we can now define a coordinate system ρ for a whole neighborhood of p. We set

$$\rho : U \times R \longrightarrow R^D \tag{31}$$
$$(x, t) \longrightarrow t\nabla\lambda(f(x)) + f(x)$$

From lemma 3 we know that the flow $\vec{j}$ will be along the the lines on which the coordinate x is constant. The flow can thus be written in the form

$$\vec{j} = \chi\vec{t}, \tag{32}$$

for some real function χ. Here $\vec{t}$ denotes the coordinate field corresponding the coordinate t. We now want to find the differential equation that governs χ. Since $\vec{j}$ is a constant source system we find

$$c = \nabla\vec{j} \tag{33}$$
$$= \nabla\chi\vec{t} \tag{34}$$
$$= \vec{t} \cdot \nabla\chi + \chi\nabla\vec{t}. \tag{35}$$

Now $\vec{t}$ is the normal unit vector to the surface given by $\lambda = \lambda_0 + t$ and its divergence is related to the mean curvature H of that surface[3]. One finds

$$H = -\frac{1}{D-1}\nabla\vec{t}. \tag{36}$$

We summarize our results in the following proposition:

Proposition 3. *Let $p \in V$ be such that $\vec{j}(p) \neq 0$ and let ρ be the coordinate system introduced in equation (31). The flow $\vec{j}$ can then be written in the form*

$$\vec{j} = \chi\vec{t} \tag{37}$$

where χ is a real valued function satisfying the differential equation

$$\vec{t} \cdot \nabla\chi - (D-1)\chi H = c. \tag{38}$$

Here H is the mean curvature of the surface normal to the vector field $\vec{t}$.

---

[3] See [2] for definitions and more details.

This proposition has a couple of important corollaries that will allow us to calculate the flow for more general examples.

Corollary 2. *Let V be a compact region in R^D. Then no characteristic that does not go through the origin intersects the boundary ∂V transversely[4] in two different points.*

Proof. Lets assume that $\sigma(t)$ is a characteristic that does not go through the origin and intersects the boundary ∂V in two points. We know from equation (3) that the flow $\vec{j}$ vanishes at these points. We will show that this is in contradiction to the behaviour of the function χ along the characteristic.

Let $\tilde{\chi}(t)$ and $\tilde{H}(t)$ be the functions χ and H evaluated on the characteristic which we parameterize by t. We assume that $t = 0$ for one of the intersection points. From equation (38) we see that

$$\frac{d\tilde{\chi}}{dt}(t) - (D-1)\tilde{\chi}(t)\tilde{H}(t) = c. \tag{39}$$

If we set

$$h(t) = \int_0^t \tilde{H}(s)\,ds \tag{40}$$

we can write the solution to (39) as follows

$$\tilde{\chi}(t) = c\,\exp\left((D-1)h(t)\right)\int_0^t \exp\left(-(D-1)h(s)\right)\,ds. \tag{41}$$

It is clear that for any finite $t > 0$ this expression is not equal to zero. Since V is assumed to be compact it follows that the t parameter will be finite when the characteristic intersects with the boundary of V again. Since the value of $\tilde{\chi}$ is not zero we obtain a contradiction to equation (3). No such characteristic can thus exist.

□

For spheres or ellipsoids all straight lines going through them intersect the boundary transversely in two points. For such regions we can calculate the flow $\vec{j}$ immediately.

Corollary 3. *Let V be a compact region in R^D with the property that every straight line that passes through the interior of V intersects the boundary ∂V transversely in two points. Then all characteristics are straight lines emanating from the origin. They are thus of the form $t\vec{r}$, where $\vec{r}$ is a unit vector.*

Proof. This follows directly from the previous corollary 2. Since all the straight lines intersect the boundary transversely they have to go through the origin. They are thus of the form $t\vec{r}$.

□

The last corollary allows us to calculate the flow $\vec{j}$ for the class of regions introduced there.

---

[4] This means that the velocity vector of the characteristic at the boundary is not included in the tangent space of ∂V at that point.

Lemma 4. *Let V be as in the previous corollary and set $d_{\vec{r}}$ to be the distance from the origin to the boundary ∂V in the direction of $\vec{r}$. Then the flow $\vec{j}$ can be written as*

$$\vec{j}(\vec{r}) = \chi_{\vec{r}}(r)\vec{r}, \tag{42}$$

where the function $\chi_{\vec{r}}$ is given by

$$\chi_{\vec{r}}(r) = \frac{c}{D}\left(1 - \frac{d_{\vec{r}}^D}{r^D}\right)r. \tag{43}$$

The quantity $\tilde{M}$ defined in equation (10) is then given by the following integral over the unit sphere

$$\tilde{M} = \frac{|c|}{D+1}\int d\Omega\, d_{\vec{r}}^{D+1}. \tag{44}$$

Proof. It follows form the last corollary that the characteristics are of the form $r\vec{r}$. The flow $\vec{j}$ can thus be written in the form of equation (42). Calculating the divergence of this equation or using equation (38) and realizing that the mean curvature is given by the inverse of the radial coordinate r we obtain

$$\frac{d\chi_{\vec{r}}}{dr} + \frac{D-1}{r}\chi_{\vec{r}} = c. \tag{45}$$

This equation can be solved immediately. The solution is given by equation (43). Finally carrying out the radial integration in equation (10) leads to the expression given for $\tilde{M}$ in equation (44). □

Example 4. For a ball of radius R we have $d_{\vec{r}} = R$, for all unit vectors $\vec{r}$. If we use this $d_{\vec{r}}$ in equation (43) to calculate $\vec{j}$ we recover equation (7).

Example 5. We next look at a two dimensional ellipse. If a and b are the main axis of the ellipse the distance $d_{\vec{r}}$ is given by

$$d_{\vec{r}} = \frac{ab}{\sqrt{b^2\cos^2\phi + a^2\sin^2\phi}}, \tag{46}$$

where ϕ is the angle that $\vec{r}$ makes with the axis of length a. Together with formula (42) and (45) this gives the flow $\vec{j}$ for the ellipse. Using equation (44) we can calculate $\tilde{M}$. We obtain

$$\tilde{M} = \frac{A^2}{\pi^2}E\left(\frac{e^2}{e^2-1}\right). \tag{47}$$

In the last formula we have expressed $\tilde{M}$ in terms of the area A and eccentricity e of the ellipse[5]. The function E is the complete elliptic integral[6].

---

[5] In terms of the parameters a and b one has $A = \pi ab$ and $e^2 = (a^2 - b^2)/a^2$.
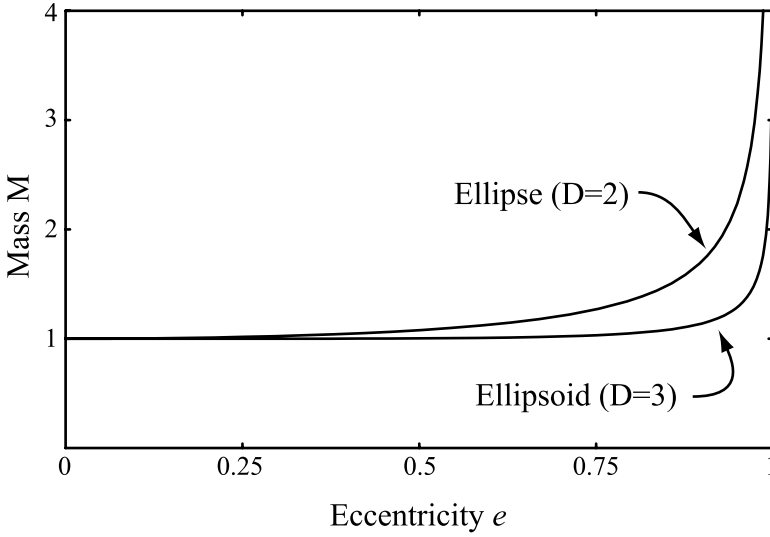[6] See [6] for more information on elliptic integrals.

Fig. 3. This graph depicts the dependence of the mass M on the eccentricity e of the ellipse or ellipsoid for a fixed metabolism. The mass has been set to one for zero eccentricity.

With this result we can investigate how for a given metabolism the mass depends on the shape of the organism. Figure 3 shows how the mass varies with the eccentricity of the ellipse. Only for very elongated shapes for which the eccentricity is close to one does one find an appreciable increase in the mass. For these shapes more and more energy is needed to sustain the transportation network.

Example 6. As a final example we want to discuss the three dimensional ellipsoid. If the axis of the ellipsoid are a, b, and c the distance $d_{\tilde{r}}$ is given by

$$d_{\tilde{r}} = \left(\sin^2 \theta \left(\frac{\cos^2 \phi}{a^2} + \frac{\sin^2 \phi}{b^2} \right) + \cos^2 \theta \frac{1}{c^2} \right)^{-1/2}. \tag{48}$$

The angles ϕ and θ are the usual polar coordinates in the coordinate system spanned by the principal axis of the ellipsoid such that x (y, z) - axis coincides with the axis of the ellipsoid having the length a (b, c respectively).

Also in this example we want to find the quantity $\tilde{M}$ corresponding to the mass of the organism. We restrict ourselves here to the case where $a = b < c$. In this case the shape is that of a rotational ellipsoid and can as in the two dimensional case be described by its eccentricity e. We obtain

$$\tilde{M} = \pi \frac{|c|}{2} \left(\frac{9}{16\pi^2} \right)^{2/3} V^{4/3} (1 - e^2)^{-1/3} \left(1 + \frac{1}{e} \operatorname{Arctanh}(e) - e \operatorname{Arctanh}(e) \right). \tag{49}$$

As in the previous example we have expressed the result in terms of the eccentricity e and the volume V[7].

---

[7] For an ellipsoid the volume V is given by $\frac{4}{3} \pi abc$.

We can again ask the question of how for a given metabolism the mass changes with the shape. The answer is given in figure 3. As in the case of the two dimensional ellipse the graph shows appreciable dependence on the shape only for values of the eccentricity that are close to one.

6. Conclusion

As it was shown in [3] the characteristics of a constant source system lead to an explanation of the allometric scaling relation found in animals and plants. The general nature of the argument explains why the scaling law holds for such a large variety of organisms of such different sizes and forms. No special knowledge of the transportation networks inside the organism are required to derive the scaling law. What is important are not the specifics of the networks but the task it has to perform. Namely to evenly supply the body with whatever it needs from a central source. This is what characterizes a constant source system and this is what is responsible for the characteristic scaling exponent.

We have derived the scaling law here for a general space dimension. To explain Kleiber's law a discussion of three dimensional space would have been sufficient. We gave the general derivation because other cases do exist in nature. An example for a two dimensional constant source system is the drainage basin of a river (for details see [1]). Another example for two dimensional constant source systems might be the leaves of plants. Since sun rays only penetrate a few layers of a leaf the task of catching sun rays is essentially a two-dimensional one. We thus conjecture that the surface area of leaves and their mass follow an allometric scaling relation as in equation (1) with a two-thirds scaling exponent. It would be interesting to see whether this prediction is true.

References

1. Banavar, J.R., Maritan, A., Rinaldo, A.: Nature, **399**, 130–132 (1999)
2. do Carmo, M.P.: *Riemannian Geometry* (Birkhäuser, Boston, 1992), p. 142
3. Dreyer, O.: to be published
4. Günther, B., de la Berra, B.L.: Acta Physiologica Latino Americana, **16**, 32–42 (1966)
5. Kleiber, M.: Physiol. Rev.,**27**, 511–541 (1947)
6. Lawden, D.F.: *Elliptic Functions and Applications* (Springer - Verlag, New York 1989)
7. McMahon, T.A.: Science, **179**, 1201–1204 (1973)
8. Peters, R.H.: *The ecological implications of body size* (Cambridge University Press, Cambridge, 1983), pp. 28–37; W. A. Calder, *Size, Function, and Life History* (Dover Publications Inc., New York, 1996), pp. 78–82, T.A. McMahon, J.T. Bonner, *On size and life* (Scientific American Books Inc., New York, 1983), pp. 64–66
9. Peters, R.H.: *ibid.*, p. 52
10. Schwartz, L.: *Mathematics for the physical sciences* (Addison-Wesley Pub. Co. Reading, Mass. 1966)
11. Warner, F.W.: *Foundations of Differentiable Manifolds and Lie Groups* (Springer - Verlag, New York 1983)
12. West, G.B., Brown, J.H., Enquist, B.J.: Science, **276**, 122–126 (1997), Nature, **395**, 163–165 (1998)